Zackenberg in a Circumpolar Context

MADS C. FORCHHAMMER, TORBEN R. CHRISTENSEN, BIRGER U. HANSEN, MIKKEL P. TAMSTORF, NIELS M. SCHMIDT, TOKE T. HØYE, JACOB NABE-NIELSEN, MORTEN RASCH, HANS MELTOFTE, BO ELBERLING AND ERIC POST

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SUMMARY

Throughout the Northern Hemisphere, changes in local and regional climate conditions are coupled to the recurring and persistent large-scale patterns of pressure and circulation anomalies spanning vast geographical areas, the so-called teleconnection patterns. Indeed, the atmospheric fluctuations described by the North Atlantic Oscillation (NAO) are closely associated with the last four decades of inter-annual variability in local snow and ice conditions observed in the Arctic. Since the NAO has also been connected with changes in the global climate, the behaviour of species, communities and other ecosystem elements at Zackenberg in relation to the NAO enables us to view these in circumpolar and global contexts.

Large-scale systems like the NAO constitute the link between the global change and local climate variability to which ecosystem components respond. Here, we place selected ecosystem elements from the monitoring programme Zackenberg Basic presented in previous chapters in a circumpolar context related to NAO-mediated climatic changes. We begin by linking the local variability in winter weather conditions at Zackenberg to fluctuations in the NAO. We then proceed by linking the observed intra- and inter-annual behaviour of selected ecosystem elements to changes in the NAO. The functional ecosystem characteristics in focus are landscape gas exchange dynamics phenological patterns at different trophic levels, consumer–resource dynamics and community stability. The influence of the NAO is presented and discussed in a broader perspective based on information obtained from other arctic localities.

The relation between the NAO and the Zackenberg winter weather is nonlinear, reflecting differential effects of the NAO as the index moves between high and low phases. The inverse hyperbolic relationship found between the NAO and the amount of winter snow was also evident as non-linear response in organisms and systems to inter-annual changes in the NAO. Responses investigated included growth and reproduction in plants and animals, population dynamics and synchrony, inter-trophic interactions and community stability together with system feedback dynamics.

I. INTRODUCTION

The implementation of the long-term ecosystem monitoring programme at Zackenberg (Zackenberg Basic) 10 years ago marked a paradigm shift in our approach to observe and record how changes in climate influence the environment. By simultaneously recording concurrent changes in the physical, biological and feedback properties of a single ecosystem, Zackenberg Basic provides an unparalleled system-level approach (Figure 1) to describe and analyse the effects of climate change integrating within-year seasonal variability as well as inter-annual long-term changes. The previous chapters in this book portray this unique multi-dimensional approach for a range of physical and biological components in the high-arctic ecosystem at Zackenberg.

Notwithstanding the uniqueness of Zackenberg Basic, ever since Charles Darwin (1859) observed that the "conditions of life may be said, not only to cause variability, but likewise to include natural selection," we have been aware that abiotic factors constitute a central component in forming the evolution and life cycle of organisms. Consequently, many previous studies have embraced, conceptually as well as empirically, the influence of weather



Figure 1 Conceptual visualisation of the interactions between climate and ecosystem responses (arrows I, II) and ecosystem feedback (arrow III).

on a wide range of species. Although many of these focused primarily on the effects of experimentally altered abiotic conditions (e.g., Chapin *et al.*, 1992), the approach of integrating retrospective data of the long-term fluctuations of species was pioneered by the studies of a handful of scientists such as the seminal work by Charles Elton (1958) and, in the arctic regions, by Christian Vibe (1967). In the early 1990s, there was a philosophical and methodological shift in the analytical approach to the study of climate effects, where the focus on local weather parameters changed to the integration of large-scale climate variability such as those described by the El Niño Southern Oscillation, the North Atlantic Oscillation (NAO) and the North Pacific Oscillation (Forchhammer and Post, 2004, and references therein). There are several important features accounted for through the integration of large-scale climate systems (Stenseth et al., 2003; Forchhammer and Post, 2004; see below) of which, the large-scale perspective of these systems enables comparisons of climatic influence on species in physically widely separated systems and, hence, an interpretation in a more global context than would be possible with the use of local weather variables only.

In this chapter, we focus on the single most important atmospheric phenomenon in the Northern Hemisphere, the NAO (Hurrell, 1996; Hurrell *et al.*, 2003; Stendel *et al.*, 2008, this volume). The chapter is divided into two conceptually different parts. The first describes the conceptual and structural perspectives of the monitoring programme Zackenberg Basic in relation to the recent compilation and synthesis of current knowledge by the Arctic Climate Impact Assessment (ACIA, 2005). The second part relates the dynamics of the NAO to the performance of a range of hierarchically selected components of the ecosystem at Zackenberg and how these are reflected in species and systems elsewhere in the Arctic. In particular, we focus on how variations in the NAO are portrayed in species-specific responses, community-level responses and ultimately, ecosystem feedback dynamics.

II. INTEGRATED ECOSYSTEM MONITORING

A. Conceptualising Zackenberg Basic: Climate Effects and Feedback

The specific responses to climate change addressed in the previous chapters may be summarised as a two-way process (Figure 1). First, any change in climate, such as increased variability in large-scale atmospheric-ocean systems or the extension of sea ice cover, will cause changes in the physical characteristics of ecosystems like snow-cover (Figure 1, arrow I). For example, the atmospheric fluctuations described by the NAO/Arctic Oscillation (AO) are closely associated with the last 35 years of inter-annual variability in snow onset, snowmelt and number of snow-free days observed in the Northern Hemisphere (Bamzai, 2003), including Northeast Greenland (Hinkler, 2005; Hansen et al., 2008, this volume; Stendel et al., 2008, this volume). Any climate-mediated changes in the physical characteristics will, in turn, affect the functioning of organisms and their interactions in the system. These effects may be divided into direct and indirect effects (Forchhammer and Post, 2004). Direct climatic effects on the organisms themselves are easily observed with no time lags. For example, from the monitoring at Zackenberg, we have learned that even small annual changes in the amount and extension of snow and sea ice have dramatic influences on. for example, seasonal growth, distribution and production of terrestrial vegetation as well as marine and freshwater plankton the following summer (Christoffersen and Jeppesen, 2002; Mølgaard et al., 2002; Tamstorf and Bay, 2002).

Indirect climatic effects, on the contrary, involve multi-organism interactions often between several trophic levels and are therefore more difficult to monitor using a single-organism monitoring approach alone (Forchhammer and Post, 2004; Forchhammer *et al.*, 2008, this volume). This has been recognised in several temporal ecosystem communities, including Zackenberg. For example, we know that following winters with much snow and prolonged ice cover on lakes, the seasonal production of freshwater zooplankton decreases dramatically in response to the low abundance of their food, phytoplankton, and not ice cover per se (Christoffersen and Jeppesen, 2002). The second aspect of the two-way interaction between climate and ecosystems is the reciprocal feedback from ecosystem to climate through changes in, for example, carbon, water and energy balances (Figure 1, arrows II and III). Documented from the work at Zackenberg and other studies, we know that changes in the physical characteristics of ecosystems are highly correlated with changes in, for example, the annual flux of carbon from system to atmosphere (e.g., Nordström *et al.*, 2001; Grøndahl *et al.*, 2007).

The monitoring programmes at Zackenberg have been purposely constructed to enable a complete spatial coverage of the general climate– ecosystems interactions portrayed in Figure 1. Indeed, the scientific structure of the monitoring programmes at Zackenberg embraces a total of 14 central themes covering the climatic (climate), physical [snow, soil, ice, sea ice, lakes, hydrology, oceanography and ultraviolet (UV) radiation], as well as biological (soil, vegetation, UV radiation effects, gas flux, lakes, arthropods, birds and mammals) ecosystem compartments (Figure 2).

B. Zackenberg Basic in a Circumpolar Context: Recommendations by ACIA

As exemplified by the previous chapters in this book, persistent climatic changes are likely to cause rather complex and, in many cases, unexpected indirect changes in arctic ecosystems confirming the conceptually visualised dynamics suggested in previous review studies (Forchhammer, 2001; Stenseth *et al.*, 2002; Walther *et al.*, 2002; Forchhammer and Post, 2004). Indeed, our ability to understand, monitor, evaluate and model the consequences of



Figure 2 Schematic landscape representation of the major scientific themes in Zackenberg Basic and how these are related to the four basis monitoring programmes: ClimateBasis (C), GeoBasis (G), BioBasis (B) and MarineBasis (M). Under each theme title the capital letters for the basis programmes involved are given. such changes requires a comprehensive synthesis of current and comprehensive knowledge of information on the observed and projected climatic effects across the Arctic.

Recently, this challenge was taken up by the ACIA, which has provided us with an unparalleled and comprehensive assessment of climate impacts based on previously observed concomitant changes in climate, terrestrial, freshwater and marine systems throughout the Arctic (ACIA, 2005). Founded upon the large amount of information provided by the assessment, ACIA has specified a range of recommendations pivotal for future climate change research in the Arctic (Table 1). These together with those proposed by the Arctic Monitoring and Assessment Programme (AMAP) in their Climate Change Effects Monitoring Programme (AMAP, 2000) and in their follow-up of ACIA (AMAP, 2005) and by the International Conference on Arctic Research Planning II (ICARP II) (Bengtsson, 2005; Callaghan 2005; Prowse *et al.*, 2005) inherently form the objective core of the monitoring at Zackenberg. Indeed, most of the monitoring activities conducted under the basis monitoring programmes at Zackenberg (Rasch et al., 2003) dovetail with the recommendations issued by ACIA embracing the long-term monitoring of cryosphere and hydrology, arctic tundra systems, freshwater systems, marine systems and UV radiation (Table 1).

The recommendations provided by ACIA are formulated in a general context; that is, actions to be taken in future climate change monitoring are not specifically addressed to be carried out within a single ecosystem. Indeed, inherent to ACIA's (ACIA 2005) notion of the need for increased spatial coverage of climate impacts, actions to be taken may be performed at different locations on selected organisms or communities without specifically monitoring the entire system in which these are embedded. In contrast and indeed as a unique additional feature, Zackenberg Basic addresses ACIA recommendations within a single ecosystem in the high-arctic region. Specifically, monitoring is performed on most physical and biological levels of the ecosystem, so that all observed changes can be functionally connected and, hence, summarised and conveyed as a holistic ecosystem response to climate changes. The current overview presented in this book has described stateof-the-art of the monitoring programme and the results it has produced so far; at the same time, to improve its potential strength, the chapter is used to evaluate the programme and tune it to become even better integrated and targeted to grasp future climate change effects in the short and longer terms (Callaghan et al., 2007).

In the remainder of this chapter we proceed by focusing on how central biological responses to climate changes at Zackenberg relate to similar responses throughout the Arctic. This is not trivial, as one of the key objectives of Zackenberg Basic is to provide a conceptual foundation for how biological and physical elements in an ecosystem react to climate, ACIA recommendations Programme Action Cryosphere and hydrology Sea ice: Fine resolution studies of Μ Satellite and photo surveillance sea ice cover in coastal waters Sea ice: Seasonal, inter-annual, None and interdecadal measurements of sea surface albedo Snow-cover: In situ measurements CG Sonic snow depth and manual of snow water equivalents in density measurements together high latitude areas with daily photo surveillance of snow extent year round Snow-cover: Measurements of CG Point measurements snow albedo over northern terrestrial regions Snow-cover: Establishment of BCG Point and spatial monitoring models to simulate snowmelt through manual, camera and satellite surveillance process Permafrost: Long-term field data G CALM on permafrost-climate interactions and on permafrosthydrology interactions River and lake ice: Improve BCG Manual hydrological monitoring understanding of hydrological and camera surveillance and meteorological control of freeze-up and break-up Freshwater discharge: Increase the С Sonic and manual hydrological network of gauge stations for monitoring monitoring discharge rates Freshwater discharge: Better None estimation of subsurface flow Arctic tundra and polar desert ecosystems Biodiversity changes: Monitor В Systematic monitoring of species currently widespread species from many taxa that are likely to decline under climate change Relocation of species: Measure В Systematic monitoring of species and project rates of species from many taxa migration Vegetation zone redistribution: В Transect and NDVI monitoring Improve information about (manual, cameras, satellite) current boundaries of vegetation zones Carbon sinks and sources: Long-G Summer and "shoulder" periods (CO₂ and CH₄) term, annual C monitoring throughout the Arctic

Table 1 Recommendations by the Arctic Climate Impact Assessment (ACIA) of relevance to the monitoring programmes at Zackenberg and their relation to the specific basis programmes

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Table 1 (continued)

ACIA recommendations	Programme	Action
Carbon sinks and sources: Models capable of scaling ecosystem processes from plot experiments to landscape scale	G	Spatial modelling
Carbon sinks and sources: Develop observatories to relate		Not relevant
Carbon sinks and sources: Combine ecosystem carbon flux estimates with C flux from thawing permafrost	G	Summer season CO ₂ monitoring over CALM plot
Ultraviolet-B (UV-B) radiation and CO ₂ impacts: Long-term impact on ecosystem of increased CO ₂ concentrations and UV-B radiation	BC	UV-B and CO ₂ monitoring
Increasing and extending the use of indigenous knowledge: Expand use of indigenous knowledge		Not relevant
Monitoring: More networks of standardised, long-term monitoring are required	BCGM	Four comprehensive programmes in operation
Monitoring: Intercated cross- disciplinary monitoring of covarying environmental variables	BCGM	This concept is the fundament for Zackenberg Basic
Monitoring: Long-term and year-round eddy covariance sites and other long-term flux sites for C flux measurements	G	Summer CO ₂ by eddy correlation, CH ₄ by chamber measurements
Long-term and year-round approach: Long-term observations are required	BCG	ClimateBasis year round, Bio- and GeoBasis seasonal
Long-term and year-round approach: Year-round observations are necessary to understand importance of winter processes	CG	ClimateBasis year round, Bio- and GeoBasis seasonal
Freshwater ecosystems and fisheries Freshwater ecosystems: Increase knowledge on long-term changes in physical, chemical and biological attributes	BCG	Physical, chemical and biological monitoring
Freshwater ecosystems: Establish integrated, comprehensive monitoring programmes at regional, national and circumpolar scales	BCG	International co-operation

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(continued)

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Table 1 (continued)

ACIA recommendations	Programme	Action
Freshwater ecosystems: Standardise international	BCG	International co-operation
approach for monitoring Freshwater ecosystems: Improve knowledge of synergistic impacts	BCG	Possible with existing data
Freshwater ecosystems: Increase understanding of cumulative impacts of multiple environmental stressors on fresh water ecosystems	В	Zackenberg Basic addresses undisturbed ecosystems
Freshwater ecosystems: Increase knowledge of effects of UV radiation-temperature interactions on aquatic biota		None
Freshwater ecosystems: Increase knowledge of linkages between structure and function of aquatic biota	В	Possible with existing data
Freshwater ecosystems: Increase knowledge on coupling among physical/chemical and biotic processes	В	Possible with existing data
Marine systems		
Observational techniques: Increase application of recently developed techniques	М	State-of-the-art equipment and techniques in use
Surveying and monitoring: Undertake surveys that are poorly mapped and whose resident biota has not been surveyed	М	No investigations like these before the establishment of Zackenberg Basic
Surveying and monitoring: Continue and expand existing monitoring programmes	М	A permanent challenge
Surveying and monitoring: Evaluate monitoring data through data analysis and modelling	М	A permanent effort
Data analysis and reconstruction: Reconstruct twentieth-century forcing field		None
Data analysis and reconstruction: Establish database with all available physical and biological data	М	Included—data can easily be provided to other databases
Data analysis and reconstruction: Recover past physical and biological data	М	Included

ACIA recommendations	Programme	Action	
Data analysis and reconstruction: Past climate events to understand physical and biological responses to climate forcing	М	Included	
Field programmes: Undertake field studies to quantify climate- related processes	М	Major purpose	
Modelling: Develop reliable regional models	Μ	Included	
Approaches: Prioritize ecosystem- based research by integrating multiple ecosystem components in models concerning climate effects	М	The concept of Zackenberg Basic	
Ozone and UV radiation UV radiation: Address the impact of increased UV irradiance	BCG	Included	

Table 1 (continued)

B, BioBasis; G, GeoBasis; C, ClimateBasis; M, MarineBasis.

applicable in any system in the Northern Hemisphere (Rasch et al., 2003; Forchhammer et al., 2007). Specifically, we may ask whether the responses observed at Zackenberg are unique or portray any mechanisms common for other systems as well. Indeed, the accumulation of biological and physical time series has recently provided us with the opportunity not only to specifically test whether species do in fact respond to changes in global climate but also, equally important, to what extent such responses vary in a large-scale spatial context (Forchhammer, 2001; Stenseth et al., 2002; Walther et al., 2002; Forchhammer and Post, 2004). Previously, results emerging from species-specific or community-level responses to local weather conditions have often extrapolated to draw conclusions as well as predictions from General Circulation Models (e.g., Oechel et al., 1997). Here, we take a different approach by integrating responses to large-scale climatic variability expressed through the inter-annual variation of climatic indices, a method rooted in an early paper by Turchin et al. (1991) in which the stochastic error term of species responses was modified to incorporate climatic conditions (Forchhammer and Post, 2004; Forchhammer et al., 2008, this volume). Before we look at how different organisms at Zackenberg and elsewhere in the Arctic respond to variations in large-scale climate, we shortly introduce the properties of such large-scale climate indices with a special focus on the ecological properties.

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III. INDICES OF LARGE-SCALE CLIMATE

A. The NAO and Its Non-Linear Properties

Extensive spatio-temporal changes in our climate are reflected in the recurring and persistent, large-scale inter-annual dynamics of the pressure and circulation anomalies covering extensive geographical areas. These so-called teleconnection patterns express statistically strong relationships with weather conditions across space and time (Stenseth *et al.*, 2003; Forchhammer and Post, 2004). For example, the winter of 1995/1996 was unusually dry in northern Europe and Russia, whereas North America and West Greenland experienced an unusually large amount of snow the same winter. These regional weather conditions could be related to a strong negative phase of the NAO (Kushnir, 1999) (Figure 3).

Although the NAO is the most prominent teleconnection pattern in the Northern Hemisphere (Barnston and Livezy, 1987) and has, during its latest transition from a low to high phase during 1965–1995, been linked to the raise of 0.21 °C in mean temperature in the Northern Hemisphere (Hurrell, 1996), a range of other important large-scale teleconnections have been identified worldwide, including the well-known El Niño Southern Oscillation



Figure 3 Long-term (1864–2006) variability in the NAO winter index; for definitions see Hurrell (1995) and Stendel *et al.* (2008, this volume). The blue line shows the time series of annual indices, whereas the red line gives the trend of the times series calculated as the smoothed spline of the raw data [i.e., non-parametric cubic B-spline with 30 degrees of freedom; see Hastie and Tibshirani (1990) for details]. Right figure: Spectral analysis of the NAO time series using the smoothed periodogram function in S-plus (spec.pgram). A smoothing window vector of c(7,7) was defined; see Venables and Ripley (1994) for details. The spectral decomposition of the NAO time series displays two peaks in the frequency spectrum at 0.43 and 0.13, respectively. This suggests that variability in the NAO dynamics may be characterised by two sets of multi-annual fluctuations, one of 2–3 years (1/0.43) and one of 7–8 years (1/0.13).

(Stenseth *et al.*, 2003). Here, we focus on the inter-annual variation in the NAO during winter (December–March) when it is most pronounced. The specific definition of the winter index and the meteorological rationale behind the NAO as well as its relation to the Northern Hemisphere Annual Mode (NAM)/AO are given in detail by Stendel *et al.* (2008, this volume). Although the winter NAO displays high inter-annual variations, it may be characterised by alternating periods of low and high phases (Figure 3). Specifically, the temporal dynamics of the winter NAO have two distinct sets of multi-annual fluctuations of 2–3 years and 7–8 years (Figure 3).

The negative and positive phases of the NAO (Figure 3) are important as they often characterise contrasting influences of the NAO on winter weather conditions (Hansen et al., 2008, this volume; Hinkler et al., 2008, this volume). For example, during the low NAO phase, 1965–1983, there was a significant positive linear correlation between winter precipitation and the NAO in Northeast Greenland (Figure 4A; Hinkler et al., 2008, this volume). In contrast, during the high NAO in 1979–1997 (Figure 3), the association between winter precipitation and the NAO became negative (Figure 4B). Note also that during high-NAO periods, the differential effect of the NAO on winter precipitation across the North Atlantic is deepened (Figure 4B). Although long-term linear associations between the NAO and winter precipitation in Northeast Greenland are found to be non-significant (Hinkler, 2005; Hansen et al., 2008, this volume), the contrasting NAO-precipitation relations over time, do suggest a non-linear association between winter weather conditions and the NAO. Indeed, over a 10-year period at Zackenberg, the snow-cover present on June 10 displayed a significant hyperbolic \cap shaped relation for high NAO indices (Figure 5A). This pattern was corroborated for the inter-annual variations in maximum snow depth (Figure 5B) as well as the date for which the snow is melted to below 0.1 m (Figure 5C) recorded at Zackenberg over the same period. Given the importance of inter-annual variations in winter precipitation and its melt-off found for the ecosystem at Zackenberg reported in previous chapters, we may expect to find similar non-linear relations between NAO and the functioning of organisms, their population dynamics and, potentially, biological interactions in the communities in which they are embedded (Forchhammer, 2001; Stenseth et al., 2002).

The latest increasing phase of the NAO (1965–1995; Figure 3; Stendel *et al.*, 2008, this volume) was associated with a dichotomous response in winter (December through March) weather conditions across the Arctic. Specifically, whereas Northeast Greenland, northern Scandinavia and Russia experienced on average warmer and wetter winters, West and South Greenland, eastern Canada and western Alaska had on average colder and



Figure 4 Map of the northern Atlantic region with Greenland centrally placed. Graded colouring indicates the degree of seasonal linear correlation (-1 to 1) between the NAO and winter (December–March) precipitation during (A) 1965–1983 (low NAO phase, mean \pm SEM: -0.45 ± 0.45) and (B) 1979–1997 (high NAO phase: 1.32 ± 0.50). The horizontal bar relates colouring and correlation coefficients. Red dot gives the location of Zackenberg on the east coast of Greenland. Analyses were performed by the NOAA-CIRES/Climate Diagnostic Center (http://www.cdc. noaa.gov).

drier winters (Figure 6A, B). As pointed out by Stendel *et al.* (2008, this volume), many of the models discussed in the latest report from the Intergovernmental Panel on Climate Change (IPCC) suggest an increase in the positive phase of the NAO and associated teleconnection patterns (Christensen *et al.*, 2007). Although the direct local effects of the NAO vary considerably, indirect effects through changes in the extension of sea ice may become increasingly important (Stendel *et al.*, 2008, this volume). Hence, we may expect that future NAO-related changes in local winter weather conditions will be as depicted in Figure 6.



Figure 5 (A) Inter-annual variation in snow-cover on June 10 (standardised) in relation to the NAO winter (December through March) index. The solid line is a non-linear generalised additive model (GAM) with 95% CIs as dotted lines; the rugplot along the *x*-axis marks the "observed" *x* values (Venables and Ripley, 1994). (B) Maximum recorded winter snow depth and (C) day of the year for snow depth below 0.1 m at Zackenberg June 2–July 17 in relation to NAO indices above 0. All R^2 vales are significant (p < 0.05). Snow data from Sigsgaard *et al.* (2006).

B. Ecological Perspectives of the NAO

Three aspects are central to our perception of how large-scale climate indices are related to the functioning of organisms and their interactions in the ecosystem. First, organisms do not respond to changes in the large-scale indices like the NAO directly but to the variations in local weather that follow changes in the NAO. Their responses embrace horizontal within-generation and vertical across-generation changes (Figure 7A; Forchhammer and Post, 2004). Within-generation responses are related to the individual's ability to respond to short-term climate changes (i.e., phenotypic plasticity)



Figure 6 Map of the circumpolar area. Graded colouring indicates the degree of seasonal linear correlation (-1 to 1) between the winter NAO and (A) winter (December–March) temperature 1965–1994 and (B) winter precipitation 1965–1994. The vertical bar relates colouring and correlation coefficients. Red dots give the location of Zackenberg on the east coast of Greenland. Analyses were performed by the NOAA-CIRES/Climate Diagnostic Center (http://www.cdc.noaa.gov).

and involve life history trade-offs such as early reproduction and senescence (Post *et al.*, in press) at the expense of somatic growth. Those individuals responding optimally to climate changes will maximise their reproductive value and bear most offspring (Stearns, 1992).

The across-generation responses of organisms to climate assumes that optimal life history strategies are genetically inherited and passed from one generation to the next through the process of adaptation (Stearns, 1992). The biological responses to changes in the NAO reported below probably integrate both types where the relative importance depends on the evolutionary background of organisms as well as the length of the study. Since the design of the monitoring programmes at Zackenberg include no genetic components, we cannot here differentiate between the two types of responses to climate (but see Høye *et al.*, 2007a).

The second aspect relates to the integrative nature of both organisms and the NAO. Although organisms at any time respond to prevailing weather and not to the indices of the NAO, many studies have demonstrated that the NAO and other similar indices seem to be better predictors than local weather (Hallett *et al.*, 2004). The answer was provided by the zoologist H.D. Picton (1984), who in many ways was ahead of his time. In his early study of climatic effects on ungulates, he realised that he needed an integrative climate index, "since animals are physiological weather integrators the

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index must allow the weather data to be integrated or summed in a fashion which approximates the net result of the manner in which the animals integrate the weather" (Picton, 1984). This was developed further with respect to the NAO by Hallett et al. (2004), who pointed out that since precipitation, strong winds and low temperatures at any time during, for example, winter may negatively affect organisms in an additive manner, most measures of local weather previously used by ecologists failed to capture this complexity. In contrast, seasonal indices of large-scale climate such as the winter NAO index integrate both the temporal and compositional aspects of weather affecting organisms (Figure 7B; Stenseth and Mysterud, 2005). For example, if a study of the effects of weather focused on the average amount of winter precipitation during January only, this would disregard any influence of precipitation in other months as well as the influence of other abiotic conditions (Figure 7B). The NAO winter index, however, would capture these variations (Figure 7B) and as such depict a far better measure of how organisms integrate weather changes in their responses.

Finally, the NAO also has the unique feature of embracing spatial variations of climate on a much larger scale than local weather measurements (Stenseth *et al.*, 2003; Forchhammer and Post, 2004; Stenseth and Mysterud, 2005). For example, the influence of the NAO on the dynamics of different populations of Canadian lynx *Lynx canadensis* across Canada varies from negative in eastern Canada to positive in central Canada to negligible in western Canada (Stenseth *et al.*, 1999). This is due to large-scale spatial differences in the atmospheric circulation characteristic of the NAO and, hence, its relation to local weather (Stenseth *et al.*, 1999). This spatial aspect of the NAO makes it particularly useful when merging the biological responses observed at Zackenberg with responses observed elsewhere in the Arctic. Below, we focus selectively on species-specific responses, communitylevel responses and ecosystem feedback dynamics in relation to the spatiotemporal dynamics of the NAO integrating the dynamics observed by the monitoring at Zackenberg.

IV. SPECIES-SPECIFIC RESPONSES

A. Vegetational Changes

1. NAO Phases Affect Growth and Carbon Fixation in Cassiope Tetragona

The white arctic bell-heather *Cassiope tetragona* is a long-lived dwarf shrub with a wide circumpolar distribution and occurs throughout Greenland, although it is confined to the inland and higher altitude in the southern regions

(Böcher et al., 1968). It is a key species in dry heath communities and forms extensive heaths in the lowland at Zackenberg on mesic ground covered by snow in winter (Bay, 1998). Despite its high abundance, *C. tetragona* is not grazed (Callaghan *et al.*, 1989). Individuals in high-arctic populations of *C. tetragona* have been estimated to be between 30 years old and 60 years old, and genets may live for several hundred years (Havström *et al.*, 1995; Johnstone and Henry, 1997). This high longevity combined with its extensive circumpolar distribution makes *C. tetragona* a suitable species for studying ecophysiological responses in high-arctic plants to large-scale spatio-temporal changes in climate. Indeed, previous retrospective analyses have showed that the annual growth of *C. tetragona* is dependent on variations in temperature, precipitation and thawing degree days, which vary geographically (Callaghan *et al.*, 1989; Havström *et al.*, 1995; Johnstone and Henry, 1997).

Combining the knowledge of annual growth sensitivity to weather conditions with isotope analyses of C. tetragona annual growth increments, Welker et al. (2005) were able to couple concurrent changes in water sources and leaf gas exchange with changes in large-scale climate mediated by the NAO/AO in a high-arctic population in eastern Canada. Welker et al. (2005) estimated the occurrence of two isotope characteristics in annual growth increments: oxygen isotope ratios (δ^{18} O) and carbon isotope ratios (Δ), where the former expresses the ratio of oxygen atoms ${}^{18}O/{}^{16}O$ (e.g., Dansgaard, 1964) and the latter expresses the ratio of carbon atoms ${}^{13}C/{}^{12}C$ in the plant relative to the ${}^{13}C/{}^{12}C$ ratio in the atmosphere (e.g., Farquhar *et al.*, 1989; Sandquist and Ehleringer, 2003). Since the δ^{18} O values are significantly lower in snowmelt water than in rain water, they were able to trace across years whether annual growth in C. tetragona was due primarily to increased uptake of water from snowmelt or rain. Furthermore, as high Δ values reflect increased carbon fixation by plants, and Δ values are higher when C. tetragona plants are exposed to increased subsurface snowmelt water (and hence decreased δ^{18} O values) throughout the summer, Welker et al. (2005) could couple the inter-annual variations in growth increments and degree of carbon fixation in C. tetragona to concurrent changes in the amount of snow. In eastern high-arctic Canada, low NAO/AO winters result in increased winter precipitation and vice versa (Figures 4 and 6; Hurrell, 1995; Bamzai, 2003). Therefore, here a negative phase of the NAO/AO will increase winter precipitation and snowmelt water use of C. tetragona, decrease δ^{18} O in plant segments, increase carbon fixation by leaves (high Δ values) and, finally, result in higher stem and leaf growth (Figure 8A). Recently, the co-isotopic approach presented above has been tested successfully using local environmental conditions (Sullivan and Welker, 2007) confirming the interaction described by Welker et al. (2005).

Although the techniques of isotope characterisation of plant growth are not implemented in the monitoring at Zackenberg, the climate-mediated ZACKENBERG IN A CIRCUMPOLAR CONTEXT



Figure 8 (A) Diagram showing the consecutive influence of negative and positive phases of the NAO/AO and growth of *C. tetragona*. Modified from Welker *et al.* (2005). (B) Annual growth of *C. tetragona* at Zackenberg in relation to the NAO. Standardised growth was estimated from the inverse relationship between the recorded changes in number of *C. tetragona* flowers and measured changes in the Normalised Vegetation Difference Index (NDVI) at *C. tetragona* sample plots (model R^2 values 0.59–0.71, p < 0.01). Current-year numbers of flowers are generally negatively correlated with current-year shoot elongation and leaf number (e.g., Johnstone and Henry, 1997). Right figure: annual standardised growth of *C. tetragona* for NAO > 0.

growth of *C. tetragona* observed here suggests that its growth is positively related to the presence of snow and, hence, large-scale climate change mediated by the NAO as described by Welker *et al.* (2005). Following winters characterised by increasingly higher NAO values, the growth of *C. tetragona*

at Zackenberg increased non-linearly (Figure 8B) similar to the relationship between inter-annual variations in winter NAO and the amount of snow recorded at Zackenberg (Figure 5). In fact, as would be predicted from the insignificant relationship between the negative NAO indices and the amount of snow at Zackenberg (Figure 5A), negative NAO indices had no significant influence on the growth of *C. tetragona* at Zackenberg (Figure 8B). The positive effect of increasing snow mediated by the NAO has also been found in *C. tetragona* populations at Svalbard. Up to 51% of the inter-annual variations in growth were explained by the NAO (Figure 9) and, as for the Zackenberg population, the effect of the NAO was most pronounced for high positive NAO values.

Three important issues emerge from the monitoring at Zackenberg and previous studies of *C. tetragona* discussed above. First, the growth of *C. tetragona* portrays a significant and consistent signal of large-scale climate mediated by the NAO across high-arctic populations of which the response seen at Zackenberg is comparable with the responses seen elsewhere. Second, as a circumpolar key species in arctic heath communities, the consistent response of *C. tetragona* to changes in the NAO may serve as an indicator for not only climate-induced changes in biomass (i.e., growth) in high-arctic heaths but also how heaths may interact with atmosphere through the concomitant variations in carbon fixation described by Welker *et al.* (2005). Third, assuming future NAO-related climate changes across the Arctic will be characterised by increasingly higher NAO winters (Christensen *et al.*, 2007),



Figure 9 Annual growth of *C. tetragona* in Adventdalen, Svalbard, estimated as the mean number of leaves per year. Data are from Callaghan *et al.* (1989). Right figure: annual growth of *C. tetragona* adjusted (last year's growth; first-order autoregression) in relation to the NAO. The solid line is a non-linear GAM with 95% CIs as dotted lines; the rugplot along the x-axis marks the "observed" x values (Venables and Ripley, 1994). The GAM explained the relationship significantly better (p < 0.04) than a general linear model.

the future performance, growth and feedback of *C. tetragona* populations may be divided into two with respect to the dichotomous arctic changes in local winter weather conditions observed in the latest increasing phase of the NAO (Figure 6). A similar division in long-term patterns of annual growth increments observed across the Arctic has been observed in another dwarf shrub species, the arctic willow *Salix arctica*.

2. Large-Scale Spatial Synchrony in the Growth of Salix Populations

S. arctica is the northernmost woody plant species. It is well adapted to the arctic, sub-arctic and alpine environment with a circumpolar distribution (Böcher *et al.*, 1968). In Greenland, it is found all the way to the northern limit of land, but is replaced by the blue-grey willow *S. glauca* south of Disko on the west coast and Jameson Land on the east coast. In contrast to the taller *S. glauca*, which is a characteristic shrub of the coastal heath (Böcher *et al.*, 1968), *S. arctica* rarely grows more than 20–25 cm in height. However, despite its small size and slow annual growth (Figure 10), *S. arctica* is a long-lived plant and is known to live for more than 100 years. For example, at Zackenberg, the oldest individual recorded was 94 years old (Schmidt *et al.*, 2006), whereas a 116-year-old individual has been recorded at Qaanaaq/ Thule in North Greenland (Figure 11).

Despite its huge potential for coupling climate changes with annual radial growth in woody dwarf shrub species, there have been few dendroclimatological studies of arctic Salix species (Schmidt et al., 2006). Instead, retrospective analyses of long-lived arctic plant species have focused on describing inter-annual variation in external features such as those for C. tetragona (Callaghan et al., 1989; Welker et al., 2005). A novel approach using microscopic examination (Figure 10) has enabled within as well as across population comparisons in annual growth of arctic dwarf shrubs. This technique was successfully applied to a large sample of S. arctica at Zackenberg and, in contrast to C. tetragona, annual radial growth of Salix was negatively influenced by increasing early spring snow-cover. Since temperature from May through August, neither monthly nor combined seasonally, had significant effects on growth of Salix at Zackenberg (Schmidt et al., 2006), NAOrelated changes in the amount of snow during winter are probably quite important. Indeed, the variations in annual growth radii have been found to correlate directly with the winter NAO for several species throughout the Northern Hemisphere, where the reported effects are usually negative to NAO-mediated increases in snow and, hence, shortening of growth season (Mysterud et al., 2003; but see Post et al., 1999).



Figure 10 Enlarged microscopic crosscut section of a *Salix arctica* sampled at Qaanaaq/Thule, West Greenland, summer 2002 (M.C. Forchhammer, unpublished data). Two consecutive dark rings (summer bark) represent 1 year of radial growth, which vary tremendously from year to year as can be seen from the two sets of connected arrows. This individual was 22 years old at the time of sampling. The narrowest annual radial growth occurred in 1984 and the individual displays low autocorrelation in radial growth across years. Photo: Claudia Baittinger. For methodological details, see Schmidt *et al.* (2006).

Climate has the potential to not only synchronise population dynamics in time (Box 1) but also induce synchrony in species-specific life history traits, such as growth and reproduction. A comparison of the annual growth of Salix at Zackenberg with other arctic/alpine Salix populations (and Betula on Svalbard) across the Arctic revealed no distinct growth dynamics, common for all populations, although the Zackenberg and Qaanaaq/Thule populations tended to have multi-annual fluctuations in their temporal growth dynamics (Figure 11) resembling those found in the NAO winter index (Figure 3). Over the last three to four decades, the synchrony of growth patterns in these populations has changed dramatically (Figure 12A). Specifically, during the period 1965–1995, when the NAO became increasingly higher, the synchrony decreased. However, from 1995 onto 2002, as the NAO became lower, the annual growth again became more synchronous across populations (Figure 12A), illustrating a clear inverse relationship between the NAO and the degree of growth synchrony across Salix/Betula populations (Figure 12B). These dynamics are probably, as for *C. tetragona*,



Figure 11 Selected time series of annual radial growth (mm) of *Salix arctica* (Qaanaq/Thule, Zackenberg), *Salix glauca* (Kangerlussuaq/Søndre Strømfjord, Oppdal (Norway) and *Betula nana* (Svalbard). Inset panels: smoothed periodograms of time series (see Figure 3 for details).

related to spatio-temporal changes in the NAO across the North Atlantic (Figure 4). High growth synchrony across the North Atlantic is found during periods with generally low NAO winters, in which the effects of the NAO on winter conditions in East Greenland become similar to those in northern Scandinavia (Figure 4A). In other words, the *Salix/Betula* populations experience similar NAO winters and hence similar growth conditions. In contrast, during high NAO periods they do not (Figure 4B), and, consequently, low growth synchrony is observed across populations (Figure 11B). It may be noted that the relationship between the NAO and growth synchrony is non-linear with negligible effects during low, negative NAO years. This is because as NAO becomes increasingly influential on local winter conditions during high phases (i.e., increased correlation, Figure 4A, B) so does the influence of the NAO on growth synchrony (Figure 12C).

Box 1

Coupling Ecological Responses in Space: The Climate Effect Ratio

As early as in 1953, the Australian statistician P.A.P. Moran recognised that climate may play a major role in coupling the dynamics of spatially distant populations. The theory he developed, which has become known as the Moran theorem (Moran, 1953; Royama, 1992), states that "if two regional populations have the same intrinsic (density-dependent) structure, they will be correlated under the influence of density-independent factors (such as climatic factors), if the factors are correlated between the regions." Hence, the more similar the effect of climate on any pair of population, the more correlated their dynamics should be (Post and Forchhammer, 2002).

The climatic scaling between any pair of spatially separated populations can be addressed specifically through the climate effect ratio. For example, consider two populations X and Y influenced linearly by density dependence and climate:

$$X_{t} = a_{0}^{\{x\}} + a_{1}^{\{x\}} X_{t-1} + C_{t}^{\{x\}}$$

$$Y_{t} = a_{0}^{\{y\}} + a_{1}^{\{y\}} Y_{t-1} + C_{t}^{\{y\}}$$
(1.1)

in which X_t and Y_t are ln-transformed densities in year t, $a_0^{\{\bullet\}}$ and $a_1^{\{\bullet\}}$ are constants and $C_t^{\{x\}}$ and $C_t^{\{y\}}$ are the climatic influences on X and Y, respectively. According to the Moran theorem, if X and Y display similar and approximate log-linear density dependence in their dynamics, then the correlation between X and Y is (Royama, 1992)

$$C_t^{\{x\}} = k C_t^{\{y\}} \tag{1.2}$$

That is, the climatic influences on the two populations are related through the coefficient k, which equals the standardised correlation coefficients between the climate conditions influencing population X and Y, respectively (Sokal and Rohlf, 1995). When climate influence is mediated through the annual variation in the NAO, as reported extensively elsewhere (e.g., Forchhammer, 2001; Forchhammer and Post, 2004), the autoregressive population models in Eq. (1.1) can be written with $C_t^{\{x\}} = \omega_1^{\{x\}} \text{NAO}_t$ and $C_t^{\{y\}} = \omega_1^{\{y\}} \text{NAO}_t$, in which $\omega_1^{\{x\}}$ and $\omega_1^{\{y\}}$ are the regression coefficients quantifying the climatic influences of the NAO on X and Y, respectively. Isolating NAO_t and substituting into Eq. (1.2) gives

$$C_t^{\{x\}} = \frac{\omega_1^{\{x\}}}{\omega_1^{\{y\}}} C_t^{\{y\}}$$

From Eq. (1.2) it then follows that the climate effect ratio, that is, $\omega_1^{\{x\}}/\omega_1^{\{y\}}$, equals the degree of climatic correlation between the two populations k. See Post and Forchhammer (2006) for further details.



Figure 12 (A) Temporal variability (1965–2002) in the synchrony of annual radial growth of *Salix* and *Betula* from the populations in Figure 11. Red line is the most parsimonious generalised additive model (GAM) describing the temporal variation in the synchrony across all populations. (B) Annual variation of synchrony in relation to the NAO, 1965–2002 ($R^2 = 0.42$). Full line is a non-linear GAM with 95% CIs as dotted lines; the rugplot along the *x*-axis marks the "observed" *x* values. Synchrony is defined as the inverse coefficient of variation in annual radial growth, 1/CV = average/standard deviation (Post and Forchhammer, 2002). (C) Following Hinkler (2005), average values of winter NAO indices were calculated for 19-year windows for

3. Normalized Difference Vegetation Index

So far we have focused on how single key species of heath communities respond across arctic/alpine populations. In a broader context, vegetation types or even on the landscape level, the Normalised Difference Vegetation Index (NDVI) has been used successfully to study vegetational impacts of large-scale climate indices, such as the NAO/AO, the North Pacific Oscillation and the El Niño Southern Oscillation (e.g., Buermann *et al.*, 2003; Gong and Ho, 2003; Gong and Shi, 2003). The NDVI expresses the greenness of vegetation and correlates with photosynthetic activity (e.g., Tucker *et al.*, 1986; Myneni *et al.*, 1995) and may, hence, be related to seasonal as well as inter-annual variations in plant biomass production (Todd *et al.*, 1998). A detailed description of the NDVI and associated derivations is given by Ellebjerg *et al.* (2008, this volume).

Vegetation covers most of the Earth's land surface and is one of the key players in influencing the global cycles of energy, hydrology and biogeochemistry. Consequently, it has for long been a major goal to describe large-scale changes in vegetation as well as the climate mechanisms behind such changes (e.g., Zhou *et al.*, 2001; Buermann *et al.*, 2003). For this, the NDVI has proven to be a most useful index to study vegetational changes. Analyses of NDVI may be performed at any vegetational level all the way from individual vegetation plots through landscape and regional vegetation dynamics to hemispheric scales. Local-scale, species-specific plot changes in NDVI are addressed elsewhere (Ellebjerg *et al.*, 2008, this volume). Here we focus on how inter-annual changes in NDVI across the landscape at Zackenberg are influenced by the NAO and how these are related to similar interactions observed throughout the Northern Hemisphere.

At Zackenberg, there is an apparent altitudinal variation in annual mean NDVI, with highest values observed between 0 m a.s.l. and 150 m a.s.l. and decreasing up to 600 m a.s.l. (Figure 13A). This, of course, is closely related to the distribution of vegetation types where those with highest growth and biomass are found on the valley floor (Bay, 1998; Ellebjerg *et al.*, 2008, this volume). A large proportion of the inter-annual variation on the landscape level could be related to changes in the NAO (Figure 13B). In particular, for positive NAO indices there was a non-linear U-shaped relationship ($R^2_{partial} = 0.41$) where increasingly higher NAO values lead to an increase in mean

the "centre years" 1968–1994. For each of these periods, R^2 values of the relationship between NAO and degree of growth synchrony across the five *Salix/Betula* populations in Figure 11 are given. These are plotted as a function of the corresponding average NAO indices. Solid line is the linear regression and dots above the dashed line ($R^2 = 0.14$) are significant (p < 0.05).



Figure 13 (A) Yearly mean NDVI for the different altitudinal regions at Zackenberg (data from M.P. Tamstorf, unpublished). There are no data available for 2003. The lowest lying altitudinal ranges did not display a significant trend (p>0.10), but the NDVI of vegetation types between 150–300 m a.s.l. and 300–600 m a.s.l. decreased significantly (r = -0.48 and r = -0.58, respectively) from 1995 to 2005. (B) Annual variations in mean NDVI in relation to the NAO. Variations in the annual mean NDVI were corrected for local variations in snow-cover and altitudinal range (see Table 2). Solid line is a non-linear GAM with 95% CIs as dotted lines; the rugplot along the *x*-axis marks the "observed" *x* values.

NDVI (Figure 13B). Integrating the contrasting NAO–snow interface, we see that the positive large-scale effect may be perpetuated through decreasing early snow-cover (Figure 5A).

However, the spatial analyses of the inter-annual variation in mean NDVI suggest that the effect of the NAO is highly dependent on altitude and hence the vegetation type in focus (Table 2). Whereas variations in the NDVI in the lowland vegetation types at Zackenberg are primarily influenced by snow-cover, the NDVI of vegetation types above 50 m a.s.l. is more affected by the

	Predictor variables			
Model type	Region	Snow-cover	NAO	Model R^2
GLM (all ranges)	42.68	3.66	0.77	0.29
GAM (all ranges)	23.89	1.82	18.01	0.66
GAM (0–50)	_	3.38	2.52	0.56
GAM (50–150)	_	0.31	3.81	0.44
GAM (150-300)	_	2.67	10.64	0.72
GAM (300-600)	_	1.52	5.04	0.52

 Table 2
 Multivariate Generalised Linear Model (GLM) and Generalised Additive

 Model (GAM) analyses of inter-annual variations in mean Normalised Difference

 Vegetation Index (NDVI) at Zackenberg as the response variable

Predictor variables are altitudinal ranges (m a.s.l.) of the valley Zackenbergdalen, snow-cover on June 10 and the NAO winter index. Altitudinal range was included in the first two full models. Since the GAM performed significantly better than GLM, GAM analyses were done for each range separately. Data from Meltofte (2006). *F*-values are given for each predictor influence as measure for each predictor's relative influence on NDVI. Bold values indicate significance (p < 0.05).

NAO (Table 2). As reported for alpine as well as temperate systems in northern Scandinavia (Pettorelli *et al.*, 2005a,b), this suggests differential large-scale climate effects across altitude (and vegetation types) at Zackenberg. In the lowland vegetation, NDVI variations are highly dependent on the topographical heterogeneity of the landscape (Hinkler, 2005) in contrast to vegetation at higher altitudes, where it is the large-scale setting of the winter by the NAO winter index which is the most influential (Table 2).

The major increase in plant growth observed in the northern high latitudes during the last 20 years (Myneni et al., 1997) is tightly coupled not only to the observed temporal dynamics of the NAO indices (Figure 3A) but also to the spatial variability in the NAO-temperature/precipitation relations (Figure 6) (Buermann et al., 2003). Similar relations and mechanisms are observed at Zackenberg (Figure 13B; Ellebjerg et al., 2008, this volume). However, at Zackenberg, the high altitude (150-600 m a.s.l.) displayed a negative trend in NDVI over the last decade. This trend is not only found in the overall NDVI data obtained from the satellite data but also in plot measurements (Tamstorf et al., in press). While winter precipitation has been variable but without significant trends, the summer temperatures and the length of the melting season have increased over the last 10 years. This has led to a decrease in the number and extent of perennial snow patches, with a resulting decline in water availability during the mid and late growing season. The effect is most pronounced at the higher levels (above 100 m a.s.l.) corresponding with the results shown in Figure 13A.

B. Life Histories: Timing of Reproduction

The temporal allocation of growth of individuals discussed above for two arctic plant species is in fact one component of many involved in the tradeoffs of species life histories. For example, in the NAO-related growth in C. tetragona on Svalbard, current-year impact of the NAO was dependent on previous year's investment in growth (Figure 9; Forchhammer, 2002). The temporal allocation of time and energy to reproduction throughout an individual's life is probably one of the pivotal components determining lifetime reproductive success (Clutton-Brock, 1988), and for many species reproduction as early as possible when conditions are favourable may be favoured over strategies of delaying reproduction (Stearns, 1992). Since the timing of life history events such as reproduction is determined not only by evolutionary history and ecosystem embedded biological interactions but also by constraints imposed by the abiotic environment (Stearns, 1992), any consistent changes in climate are expected to affect reproduction trends (Forchhammer, 2001). Indeed, following the last two decades of winter warming, an increasing number of studies throughout the Northern Hemisphere report increasingly earlier dates of reproduction for a range of evolutionarily distinct species of plants and animals (Forchhammer et al., 1998; Post and Stenseth, 1999; Root et al., 2003; Menzel et al., 2006; Cleland et al., 2007; Høye et al., 2007b). Many of these observed phenological changes have been related to the trend as well as inter-annual variability in the NAO winter index (Forchhammer et al., 1998; Post et al., 2001; Menzel, 2003).

Although variability exits among the most recent large-scale climatic models, one common predictive feature is the latitudinal increase in future warming where the high-arctic regions, including the area at Zackenberg, are expected to experience the fastest and greatest warming (Christensen et al., 2007; Stendel et al., 2008, this volume). Until recently, it was not known whether a similar latitudinal gradient in species responses to warming existed. Indeed, so far most long-term phenological studies had been confined primarily to temperate Europe and North America (e.g., Root et al., 2003; Menzel et al., 2006). However, using the extensive amount of data from the monitoring programme at Zackenberg, Høye et al. (2007b) showed that a wide range of high-arctic plant, insect, and bird species at Zackenberg displayed a considerable plasticity in their annual timing of reproduction concurrent to the pronounced directional change in spring snowmelt and summer air temperature at Zackenberg (Figure 14; Hansen et al., 2008, this volume). On average, the initiation of annual breeding, that is, the date of flowering in plants, emergence of insects and egg-laying in birds, advanced by 14.5 days/decade since 1995. This average value embraced an impressive range of temporal responses within as well as across species. For example, in one plot at Zackenberg, the flowering of S. arctica had advanced by more



Figure 14 Temporal trends in the mean June and July air temperature (2 m a.s.l.) measured at Zackenberg 1996–2006. Solid regressions lines are based on all data (June: slope = 0.04 ± 0.05 °C/year, $R^2 = 0.05$, p = 0.51; July: slope = 0.25 ± 0.08 °C/year, $R^2 = 0.49$, p = 0.01) and the dashed regression lines exclude the circled 2006 data (June: slope = 0.11 ± 0.04 °C/year, $R^2 = 0.43$, p = 0.04; July: slope = 0.28 ± 0.10 °C/year, $R^2 = 0.50$, p = 0.02). The period analysed by the dashed regressions is the period covered by Høye *et al.* (2007b). Data from Sigsgaard *et al.* (2006) and M. Tamstorf (unpublished data).

than 3 weeks since 1995, whereas no or little advancements were observed in other plots (Høye *et al.*, 2007b). Similar ranges of timing of reproductive phenology were observed in other species. This spatial variability in phenological responses was related to the influence of the variable landscape topography at Zackenberg, which creates considerable variation in local timing of spring snowmelt (Høye *et al.*, 2007b).

Whether phenological changes in reproductive responses display trends or not, they may nevertheless still be influenced by large-scale climate. Indeed, first egg-laying dates of sanderling Calidris alba, which showed no significant decadal trend, clearly responded to annual changes in the NAO, where increased NAO associated with increased snow and later snowmelt (Figure 5) was associated with later initiation of egg-laying by sanderlings (Figure 15A). Similarly, reproduction in the long-tailed skua Stercorarius longicaudus and musk ox Ovibos moschatus populations at Zackenberg was influenced by the NAO (Figure 15B, C). The important point here is that species do not necessarily have to display trends in their phenology in order to display a response to variations in large-scale climate. Indeed, whereas trend analyses of species responses focus on average temporal changes, analyses employing the inter-annual dynamics of large-scale systems like the NAO also integrate variability. Along with the expected increased trends, increased variability is also expected in the future climate scenarios with more extreme events (Christensen et al., 2007). Therefore, it becomes important to embrace responses to average as well as variance in climatic changes; in fact, it may be



Figure 15 Inter-annual variations in reproductive performance of selected species at Zackenberg. (A) Sanderling *Calidris alba*, median first egg-laying date (day of the year June 4–24), (B) long-tailed skua *Stercorarius longicaudus*, nest success and (C) musk ox *Ovibos moschatus*, number of calves per female. All R^2 values are significant (p > 0.05). Data from Meltofte (2006).

argued that increased frequency of extreme weather may impose an even greater constrain on organisms than merely average changes.

C. Population Dynamics

Both short-term phenotypic responses as documented above and long-term inter-generational adaptive changes in life history strategies will lead to changes in population dynamics (Figure 7A). Since the NAO has been coupled to such changes in many species (e.g., Forchhammer, 2001; Mysterud *et al.*, 2003), we may expect to find the influence of the NAO portrayed in their

population dynamics as well. In a spatial as well as temporal context, the dynamics of ungulate populations in relation to large-scale systems like the NAO are probably the best described and analysed so far.

At Zackenberg, the only ungulate species present is the musk ox, which occurs in large numbers throughout the Zackenberg area (Forchhammer et al., 2008, this volume). Here, its population dynamics are highly dependent on changes in snow-cover and, hence, length of the plant growth season (Forchhammer et al., 2008, this volume). The significant relations between the NAO and calves produced per female (Figure 15C) suggest a delayed influence of climate on the population level as the production and recruitment of offspring into a population depends on their survival to maturity (Forchhammer et al., 2002). For musk oxen, the average age of first reproduction is their third year (e.g., Olesen et al., 1994), and, indeed, long-term dynamics of the musk ox population at Zackenberg display a 3-year delayed influence of the NAO, where an increased NAO-mediated amount of snow had a delayed negative influence on population dynamics (Forchhammer et al., 2002). Although this was a shared feature in all musk ox populations in Greenland, the numerical influence of the NAO decreased from south to north (Figure 16A; Forchhammer et al., 2002).

Similar delayed effects of the NAO were found on the caribou *Rangifer tarandus* in West Greenland and could, as in musk oxen, be related to the fecundity and survival/recruitment of offspring (Forchhammer *et al.*, 2002).



Figure 16 (A) Latitudinal variation in the 3-year delayed influence (co-variate regression coefficients) of the NAO on the dynamics of the five recognised indigenous musk ox populations in Greenland; $R^2 = 0.76$, p < 0.05 (adapted from Forchhammer *et al.*, 2002). (B) Relation between the degree of pairwise cross-correlation between caribou and musk ox populations in Greenland and the ratio of the effect of the NAO on the dynamics of each population ($R^2 = 0.42$, p < 0.001). Modified from Post and Forchhammer (2002). See also Box 1 for the description and calculation of climate effect ratios.

In fact, this delayed NAO effect was also found throughout most of the Russian caribou populations, portraying the spatial variation in the NAO-local weather relations (Post and Forchhammer, 2006). Interestingly, Post and Forchhammer (2002) observed that the higher cross-correlation between the dynamics of two arctic ungulate populations, the more similar were the effects of the NAO on these populations, that is, the NAO climate effect ratio (Box 1) approached 1 (Figure 16B). In contrast, the more the NAO effects deviated among populations, the lower cross-correlation was observed (Figure 16B). This also applied for comparisons between caribou populations in West Greenland, Finland and Russia (Post and Forchhammer, 2006). The considerable geographical area in which the NAO affects arctic ungulate populations emphasises the ability of large-scale climate systems to synchronise the dynamics of physically separated populations and, thereby, their roles as potentially important drivers affecting the probability of multipopulation extinctions (Post and Forchhammer, 2006).

V. COMMUNITY-LEVEL RESPONSES

A. Consumer–Resource Interactions

Changes in climatic conditions affect simultaneously all the organisms embedded in a community or an ecosystem. Therefore, any correlation between climate and the performance of a single species may also embrace changes in its interaction with other species such as its competitors and consumers (see also Berg et al., 2008, this volume; Forchhammer et al., 2008, this volume; Schmidt et al., 2008, this volume). For instance, in addition to the direct effects of the NAO on the reproduction and population dynamics reported above, a previous study from Zackenberg showed that an indirect influence of the NAO on the musk ox population occurred through its interaction with its main plant forage, S. arctica (Forchhammer et al., 2005). At Zackenberg, the inter-annual variation in snow-cover is mediated through the NAO (Figure 5). Such changes in snow-cover may, through effects on both musk ox density and S. arctica growth dynamics, affect the distribution of foraging musk oxen in the valley Zackenbergdalen. Using general additive models (Venables and Ripley, 1994), Forchhammer et al. (2005) found complex cascading inter-trophic effects of the NAO with stepwise indirect and non-linear consequences for the spatial dynamics of musk ox foraging behaviour. Specifically, high NAO winters were associated with decreased snow-cover, which increased both the biomass and degree of spatial synchrony in growth of Salix the following summer (Figure 17A, B). Increased spatial synchrony of Salix growth, in turn, increased the spatial dispersion of musk oxen, but decreased the herd size in the same summer (Figure 18A, B), whereas no NAO-mediated effects on musk ox density affected their distribution in the landscape (Forchhammer *et al.*, 2005).

The results from Zackenberg are not unique in that large-scale climate influences have been documented in a range of communities throughout the Northern Hemisphere (e.g., Post and Stenseth, 1999). Like the musk oxen at



Figure 17 Annual biomass production (A) and synchrony (B) of *Salix* growth as a function of percentage of early spring snow-cover (June 10). Biomass is expressed through the Normalised Difference Vegetation Index (NDVI) and synchrony as the reverse coefficient of variation. Modified from Forchhammer *et al.* (2005).



Figure 18 (A) Seasonal changes in the distance between herds as a function of the degree of synchrony (1/CV) in the growth *Salix arctica* in the study area. (B) Variations in herd size as a function of the degree of synchrony in the growth *S. arctica*. Full line is the second-order polynomial generalised additive models with 95% CIs as dotted lines; the rugplot along the *x*-axis marks the "observed" *x* values. Modified from Forchhammer *et al.* (2005).

Zackenberg, changes in the NAO affected the seasonal distribution of red deer *Cervus elaphus* populations in Norway through influences on plant biomass (expressed by the NDVI) (Pettorelli *et al.*, 2005a). Red deer populations migrate seasonally between summer areas in the highlands and winter areas in valleys. As it turns out, increasing NAO corresponded to less snow at lower altitudes but more snow at high altitudes, which, in turn, resulted in spatially more variable plant phenology, offering migrating deer a longer period of access to high-quality forage. This led to increased body mass (Pettorelli *et al.*, 2005a), which eventually affected the structure as well as dynamics of populations (Post and Stenseth, 1999).

Another example of such NAO-mediated impacts on consumer-resource interactions comes from the well-studied tri-trophic predator-prey-plant system on Isle Royale in North America (e.g., Peterson et al., 1984). Here, inter-annual fluctuations in the NAO affected not only each trophic level directly (Post and Forchhammer, 2001) but also the social behaviour of wolves Canis lupus and, hence, their hunting efficiency, which had indirect consequences for both the moose *Alces alces* population (delayed negative) and growth (delayed positive) of the forage most important to moose, balsam fir Abies abies (Post et al., 1999; see also Forchhammer et al., 2008, this volume, for further details). The population dynamics of moose were primarily controlled by the top-down effect from wolves (33%), followed by the direct climate effect, that is, NAO (14%), and bottom-up from fir to moose (10%) (Wilmers et al., 2006). In 1981, there was an outbreak of canine parvovirus in the wolf population (Peterson et al., 1998), that is, a fourth trophic level was introduced to the system on Isle Royale. This had striking effects on climatic and trophic drivers of the moose population. First, in the transient dynamics, the direct effects of the NAO became the most important factor (37%). And secondly, the bottom-up effect became more important (22%) than top-down influence (1%) (Wilmers et al., 2006).

B. Stability of Species Populations and Interactions

It follows, from the above, that together with the influence of density dependence and direct climatic effects on each species' population dynamics, any shift in consumer–resource interactions may greatly influence the effects of climate and, hence, the stability of both populations and communities. Conceptually, the dynamics of populations in a stochastic environment is a combined result of the stabilising influences of density dependence and destabilising influence of the extrinsic stochastic factors such as climate (e.g., May, 1973, 2001). The Zackenberg musk ox population is characterised by medium direct density dependence and a strong influence of the NAO (Figure 19A), which suggests that whereas the population may be destabilised



Figure 19 (A) Comparing strength of direct density dependence (first-order autoregressive coefficient) and the effect of NAO (additive co-variate coefficient) across five musk ox populations in East Greenland. Data from Forchhammer *et al.* (2002). (B) The tri-trophic system at Zackenberg embracing arctic wolf, musk ox and arctic willow after the wolf re-invasion to East Greenland in the early 1970s (Dawes *et al.*, 1986). For each trophic level is given the direct density dependence and the direct effect of snow-cover. Data from Schmidt (2006).

by the NAO, this is counteracted by a high level of density dependence in that population. This has been documented as well for caribou throughout West Greenland, Finland and Russia, where a clear inverse relationship between density dependence and the contribution of the NAO to dynamics was found across all populations studied (Post, 2005). Comparing across the musk ox populations in Northeast Greenland, the decreasing trend in the effect of the NAO and the increasing trend in direct density dependence from south to north (Figure 19A) indicate that the most stable populations are the northernmost.

Focusing on the tri-trophic system of arctic wolf *Canis lupus arctos*, musk ox and *S. arctica* at Zackenberg, we see that the strongest self-regulation, that is, direct density dependence, is found on the intermediate trophic level (musk ox), whereas the strongest influence of climate is found at the bottom trophic level of plants (Figure 19B; Schmidt, 2006). Therefore, the influence of future changes in climate on the predator–prey–plant system at Zackenberg is expected to be primarily a bottom-up process, where the influence of climate on the growth and performance of *S. arctica* is expected to spread through the system mediated by the trophic interactions of musk oxen and wolves (Schmidt, 2006). Similar system dynamics emerges from another study on the tri-trophic predator–prey–plant system on Isle Royale, where analyses similar to those at Zackenberg showed that although self-regulation was present at all three trophic levels, the greatest climatic impact was found at the bottom and top levels (Post and Forchhammer, 2001).

The stability of multi-level trophic systems and, hence, their vulnerability to climate and other stochastic environmental fluctuations have, theoretically as well as empirically, been shown to depend on the diversity of species in the systems, where increased diversity increases system stability (e.g., Pimm, 1984; Tilman and Downing, 1994; Tilman, 1996; Wilmers *et al.*, 2002). At first hand, analyses from Zackenberg support this notion. Indeed, as the wolves reappeared at Zackenberg in 1979 after 40 years of absence, the shift from a bi-trophic to a tri-trophic system was followed by an increase in stability (Figure 20; Schmidt, 2006). However, concurrent with but independent of the invasion of wolves, there was a shift in population dynamics of musk oxen and the performance of *S. arctica*, which correlated with an increased snow-cover (Schmidt, 2006). Hence, the observed change in stability may also relate to changes in the dynamic complexity (i.e., self-regulation and stochastic influence) of the individual trophic levels of musk ox and plants following a shift in the extent of snow-cover.

As conceptually demonstrated by May (1973) and later empirically by Tilman (1996), system stability increases with species diversity, whereas stability of populations does not necessarily do so. For a large temperate plant community, this dichotomy was related to extrinsic perturbations, such as shifts in climate, which affected competing species differently and, hence, increased the variability in species abundance, but at the same time stabilised plant community biomass due to decreased inter-specific competition (Tilman, 1996). Although the fundamental mechanisms shaping system stability may be similar across systems, it is reasonable to ask to what extent the



Figure 20 Community stability properties of the bi-trophic (musk ox-willow; red circle) and the tri-trophic (wolf-musk ox-willow; blue circle) system at Zackenberg. The shaded area denotes the area of stability (May, 2001). The x and y values are calculated as the trace (trB) and determinant (detB) of the community matrix **B**, respectively. For details, see Schmidt (2006).

spatial variations in population stabilities in the same species, as demonstrated for musk oxen in Northeast Greenland (Figure 19A), may influence system stability across different locations. To answer questions like this, the species-specific and multi-trophic monitoring approach at Zackenberg will become important.

VI. ECOSYSTEM FEEDBACK

A. Seasonal Impact on Annual Carbon Balance

In recent years, arctic terrestrial ecosystems have attracted major attention in the context of global carbon cycling (ACIA, 2005; Millenium Ecosystem Assessment, 2005). A reason for this is that arctic terrestrial ecosystems store a significant proportion of the global stock of soil organic carbon (C). In the arctic tundra proper, some 121–191 GT of C are stored, or $\sim 12-16\%$ of the estimated world total (McKane et al., 1997; Tarnocai et al., 2003). If boreal ecosystems are included, this estimate rises to almost 30%. The predicted significant climate changes and the feedbacks they engender could change the climatic conditions that have allowed the development of such large soil C stocks in the Arctic (Gorham, 1991; Shaver et al., 1992; McKane et al., 1997; Hobbie et al., 2000). Extensive regions of the High Arctic such as much of the Zackenbergdalen that lack substantial C stocks and currently have very limited rates of atmospheric exchange could develop dynamic C cycles. Climate-driven changes in plant community structure, specifically shifts from herbaceous and cryptogamous dominance to systems dominated by ericaceous and woody species, are also likely to change ecosystem C dynamics and balance.

Arctic soils are often wet and, when waterlogged, become anoxic. Anaerobic soils often accumulate C in the form of peat (Gorham, 1991; Clymo *et al.*, 1998) and release methane (CH₄), a radiatively important trace gas (Matthews and Fung, 1987; Joabsson and Christensen, 2001; Öquist and Svensson, 2002). CH₄ flux is rarely a quantitatively important component in the ecosystem C balance, but it can play a disproportionately important role in terms of greenhouse gas forcing (gram for gram CH₄ in the atmosphere has 23 times the radiative forcing potential of CO₂).

Greening of the High Arctic and changes in the wetness of soils are two examples of climate-driven changes that in turn cause ecosystem feedback mechanisms that involve changes in greenhouse gas exchanges (CO₂ through changed carbon storage and CH₄ through changed extent of wet soil conditions), which potentially can have important inherent feedback effects in the climate system. In addition to such changes there are also feedback mechanisms associated with changes in the energy exchange as a consequence of changed vegetation composition and structure affecting reflective properties both in the summer and through impacts on snow-cover in the winter.

Within each of the four seasons, there are important, and at times very different, processes acting, which are resulting in the net effect of the individual seasons on the annual ecosystem C budget. Critical facets of early-season conditions—such as a substantial C loss during spring melt and early summer due to release of trapped CO₂, and possibly a hindered onset of photosynthesis due to dry early summer conditions-can seriously affect the annual budget. In midsummer again water deficit can be important as a limiting factor for photosynthesis, while a very warm summer has the potential to stimulate respiration (including root respiration) more than photosynthesis (in particular in dry years), so that these effects together can be very important for the annual budget (Crawford et al., 1993; Marchand et al., 2005; Kwon et al., 2007). In the third season, a mild autumn followed by the delayed appearance of a consistent snow-cover could be critical for processes involved in C fluxes. Usually, photosynthesis will decline regardless of warm "Indian" summer conditions, which will on the contrary stimulate respiration for as long as the soils remain unfrozen (or contain free water). So a mild autumn may also be a very important triggering factor for C losses on an annual basis. Most of these seasonal aspects that may determine the annual balance are affected by NAO/AO oscillations and there may therefore also be links between these cyclic dynamics and the variations in ecosystem C balance and CH₄ emissions.

B. Carbon Flux at Zackenberg and Relations to the NAO

As discussed in detail by Grøndahl *et al.* (2008, this volume), the accumulated CO_2 during the growing season in the heath ecosystem at Zackenberg is strongly correlated with the date of snowmelt, which is related to the NAO (Figure 5). This is similar to patterns observed in peat lands of northern Scandinavia (Aurela *et al.*, 2004). However, this correlation does not necessarily translate into the annual balance, as the respiration may be strongly affected by other factors during the autumn and winter, and this may in some cases be more important for the annual budget (Vourlitis and Oechel, 1999; Johansson *et al.*, 2006). Although the sample size for investigating the interannual effects of the NAO on the net ecosystem exchange (NEE) together with other environmental factors (Grøndahl *et al.*, 2008, this volume) may be considered small, a simple comparison suggests NAO-mediated NEE dynamics, where, as would be expected from the NAO-snow relationship (Figure 5), increasing NAO winters are followed by growing seasons with higher NEE (Figure 21); that is, increased, NAO-mediated snow-cover



Figure 21 Inter-annual variations in the net ecosystem exchange (NEE; g C/m²) as function of the NAO. Data from Sigsgaard *et al.* (2006) and M.P. Tamstorf (unpublished). The solid line is a non-linear GAM with 95% CIs as dashed lines. Model $R^2 = 0.92$, p < 0.05. The rugplot along the *x*-axis marks the "observed" *x* values. Note that the positive values on the secondary axis (NEE) represent growing season net carbon uptake, and also that only the increasing trend with positive NAO values is significant.

reduces the cumulative tundra uptake of carbon dioxide the following summer.

Unlike the relatively simple relationships found in relation to parameters explaining inter-annual variability in growing season carbon uptake, the controls on accumulated CH_4 emissions are seemingly more complex. Zackenberg was the first site in the circumpolar north where it was clearly demonstrated that there are important interactions between plant species composition and potential CH_4 emissions (Joabsson and Christensen, 2001; Ström *et al.*, 2003). Any effect on plant species composition is direct through a changed climate or indirect through changes in grazing pressure, and preference of grazers may therefore affect potential emissions. Such interactions between activities at different trophic levels with ecosystem functioning in the form of trace gas exchanges are so far only very poorly understood, but Zackenberg represents an ideal setting for investigating these issues further.

Preliminary data from a newly established (from 2006) automatic CH₄ flux monitoring system combined with earlier manual data are indicating that no single parameter can explain the inter-annual variations. In other wetland ecosystems, seasonal and spatial variations in CH₄ flux are often found to correlate well with the water table position (e.g., Whalen and Reeburgh, 1992; Daulat and Clymo, 1998), and wet tundra and peat land ecosystems with substantial emissions including the fen area in Zackenberg show a nice, both large-scale spatial and temporal, correlation with mean temperatures during the growing season (Christensen *et al.*, 2003). At Zackenberg, the local spatial variability in CH_4 fluxes is high (Christensen *et al.*, 2000) and as mentioned above, dependent on interactions between temperature, water table position and vascular plant species-specific functioning. It is nevertheless most likely that drier conditions will lower the CH_4 emissions both directly through restricting the anaerobic soil layers where the CH_4 is produced (and increase the oxidised zone) and indirectly through shifts towards grassland plant species that are not stimulating CH_4 emissions to the same extent as many wetland species do (Ström *et al.*, 2003).

VII. CONCLUSIONS

The monitoring in Zackenberg Basic not only complies with most of the recommendations by ACIA but also moves beyond by providing, as recommended by ICARP II (Callaghan, 2005; Prowse *et al.*, 2005), new pivotal knowledge of (1) how an entire arctic ecosystem responds to climate variability and changes and (2) how these cascade through the system as direct and indirect impacts (Figures 1 and 2). The knowledge gained from system monitoring at Zackenberg may therefore constitute a major and unique contribution to forthcoming revisions of the ACIA recommendations.

In a climatic perspective, Zackenberg is geographically located at the boarder between the two contrasting climate regions associated with the atmospheric dynamics of the NAO. As such, the relationship between local weather conditions at Zackenberg vary non-linearly with the NAO as its inter-annual as well as long-term dynamics move between the different phases (Figures 3-5; Hansen et al., 2008, this volume; Hinkler et al., 2008, this volume; Stendel et al., 2008, this volume). Because of their integrative nature, large-scale climate systems, like the NAO, provide a suitable skeleton for studies of climate effects on different organisms at different trophic levels across the Arctic. Furthermore, this combined with an integrated system monitoring, such as Zackenberg Basic, presents a unique opportunity for describing and evaluating cumulative system responses. However, monitoring programmes with long-term perspectives, like the Zackenberg Basic, would benefit from a combined monitoring of phenotypic and genotypic responses to climate changes. Long-term observations of climate change effects will embrace both (Figure 7A), but, currently, only the phenotypic aspect is included in Zackenberg Basic.

The influence of the NAO on species dynamics and performance at Zackenberg is evident and does provide a mechanistic description of how arctic organisms respond to large-scale climate representative in a circumpolar perspective. At Zackenberg, the signature of the NAO is found in species ranging from plants to large-bodied mammals as well as in the interactions across trophic levels and system feedback dynamics to the atmosphere. Whether system stability in a changing climate pertains to the complexity of dynamics among species at the individual trophic level and/or the complexity of food webs provides an interesting pursuit in future research (Post and Forchhammer, 2001) based on using integrative system data like those provide by Zackenberg Basic.

ACKNOWLEDGMENTS

The monitoring data used in this chapter were provided by the BioBasis programme, run by the National Environmental Research Institute, University of Aarhus, and financed by the Danish Environmental Protection Agency, Danish Ministry of the Environment. The Danish Polar Center provided access and accommodation at the Zackenberg Research Station during all the years. We extend our sincere thanks to the referee, Johannes Kollmann, who contributed significant improvements for an earlier version of the manuscript.

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